



Response of ecosystem carbon fluxes to drought events in a poplar plantation in Northern China

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ABSTRACT

Poplar plantations are widely used for timber production and ecological restoration in northern China, a region that experiences frequent droughts and water scarcity. An open-path eddy-covariance (EC) system was used to continuously measure the carbon, water, and energy fluxes in a poplar plantation during the growing season (i.e., April–October) over the period 2006–2008 in the Daxing District of Beijing, China. We examined the seasonal and inter-annual variability of gross ecosystem productivity (GEP), net ecosystem exchange (NEE), and ecosystem respiration (ER). Although annual total precipitation was the lowest in 2006, natural rainfall was amended by flood irrigation. In contrast, no supplementary water was provided during a severe drought in spring (i.e., April–June), 2007, resulting in a significant reduction in net ecosystem production (NEP = −NEE). This resulted from the combined effects of larger decrease in GEP than that in ER. Despite the drought-induced reduction in NEP, the plantation forest was a strong carbon sink accumulating 591 ± 62 , 641 ± 71 , and 929 ± 75 g C m^{−2} year^{−1} for 2006, 2007, and 2008, respectively. The timing of the drought significantly affected the annual GEP. Severe drought during canopy development induced a lasting reduction in carbon exchange throughout the growing season, while the severe drought at the end of growing season did not significantly reduce carbon uptake. Additionally, irrigation reduced negative drought impacts on carbon sequestration. Overall, this fast growing poplar plantation is a strong carbon sink and is sensitive to the changes in environmental conditions.

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1. Introduction

Tree plantation establishment is one approach to sequestering atmospheric carbon to mitigate climate change (Vitousek, 1991; Wright et al., 2000). Fast growing trees, such as poplars (i.e., *Populus* sp.), which account for about 14% of the total tree plantations in China (Chinese Forestry Society, 2003), play a vital role in timber production, bioenergy, urban greening, desertification control, reforestation and carbon sequestration. However, the tradeoffs between carbon gain and water use need to be evaluated as plantations typically have higher productivity as well as higher transpiration and rainfall interception (Jackson et al., 2005). Therefore, studies of carbon flux in poplar plantations are important to

understand and quantify the carbon sequestration potential and to determine how future climate change may impact the carbon budgets.

Projected increase in the frequency and severity of droughts in the mid and high latitudes (Trenberth et al., 2007; Thomas et al., 2009) is likely to have significant implications on the carbon cycle (Granier et al., 1999; Ciais et al., 2005; Kljun et al., 2006). In addition, variation in precipitation has a strong influence on ecosystem carbon exchange (Law et al., 2002; Grünzweig et al., 2003; Ewers et al., 2007; Noormets et al., 2008, 2010) as water and carbon are closely linked in forest ecosystems (Sun et al., 2011a,b). Both gross ecosystem productivity (GEP) and ecosystem respiration (ER) may be constrained by low soil moisture during periods of drought (Scurlock and Olson, 2002; Huxman et al., 2004; Granier et al., 2000, 2007; Meir et al., 2008; Baldocchi, 2008; Bonal et al., 2008; Yuan et al., 2010). The suppression of GEP is caused by a physiological response to limited plant-available water (Meir et al., 2009; Meir and Woodward, 2010) and by structural changes of the tree during the drought (Le Dantec et al., 2000; Amthor and Baldocchi,

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2001; Reichstein et al., 2002, 2003). However, there are contradictory findings as to whether GEP and ER have similar sensitivities to drought. Goulden et al. (1996) found that ER was more sensitive to reduced soil moisture than GEP. Reichstein et al. (2002) reported that droughts affecting only surface soil can suppress ER more than GEP because GEP depends more on deep water storage. Conversely, net ecosystem exchange (NEE) may be quite unaffected by a drought if ER and GEP respond proportionally, as was the case in the old aspen forest in British Columbia, Canada (Barr et al., 2007).

In 2004, the United States – China Carbon Consortium (USCCC) was established, and a network of eddy flux measurements was installed to compare environmental controls on key ecosystems in China and the US (Sun et al., 2009). The study site used in this paper is part of the USCCC and located in the Daxing District of Beijing City, China. Results for water and energy fluxes of this poplar plantation have been previously reported (Liu et al., 2009). This paper focuses on carbon flux and balances for a 3-year (i.e., 2006–2008) period. The large variability in the timing and intensity of drought for the study period provided an unique opportunity to examine the ecosystem response to water stress and management. Our objectives of this study are to: (1) quantify the seasonal and inter-annual variability of GEP, NEE, and ER of a poplar plantation; and (2) examine the impact of drought on the variability of the carbon fluxes.

2. Materials and methods

2.1. Study Site

This study was carried out in a managed poplar (*Populus euramericana* cv. “74/76”) plantation at the Daxing Forest Farm (116°15′07″E, 39°31′50″N) in the suburb of Beijing, China. The trees were planted in 1998 at 3 m × 2 m spacing, and dead or low-vigor trees were replanted between 2001 and 2003. By the end of 2008, the average height of the trees was 14.8 ± 1.2 m (mean ± SD) and the mean diameter at breast height (DBH) was 13.8 ± 1.8 cm. The leaf area index (LAI) of the stand was 2.1 ± 0.6. Shrubs were present at low density under the canopy due to manual removal. Perennial herbs included *Chenopodium glaucum* Linn., *Medicago sativa* L., *Melilotus officinalis* (L.) Lam., *Salsola collina* Pall., and *Tribulus terrestris* L.

The climate is temperate continental with mean annual temperature of 11.5 °C, and maximum and minimum extreme temperatures of 40.6 °C and –27.4 °C, respectively (1990–2009). The average annual frost-free time period is 209 days. On average, there are 2772 mean sunshine – hours per year with 15.5 MJ m⁻² d⁻¹ of incoming solar radiation. The average wind speed is 2.6 m s⁻¹ from variable directions. Annual rainfall varies between 262 mm and 1058 mm with a long-term average of 569 mm (1952–2000). About 65% of the precipitation occurs between July and September (Daxing Weather Station, 116°19′56″E, 39°43′24″N).

The top two meters of the soil profile is largely composed of well-drained fluvial sand with a pH of 8.3 and bulk density of 1.45 g cm⁻³. The soil porosity is about 40% and capillary porosity is 32%. The terrain is flat with an average elevation of 30 m above sea level. The groundwater table decreased from 15.3 m below the ground surface in 2003 to 18.5 m in 2008, at an average rate of 0.6 m per year. Most of the reduction in the water table is attributed to local water withdrawal for crop irrigation (Zhang et al., in preparation).

Management operations, such as flood irrigation and tilling, were applied from time to time since the establishment of the plantation but not well documented. During our study period from 2006 to 2008, the irrigation was applied only during the growing season (i.e., April–October) in 2006 and machine tilling applied once for weed suppression at the end of July in 2006. The amount

of irrigation water was recorded every week by the water meters from three wells. It was calculated that in 2006, 35 mm of water was applied in April, and 21 mm of water was applied in May.

2.2. Flux and meteorological measurements

Micrometeorological measurements at the site included net radiation (R_n) and photosynthetically active radiation (PAR) at 16 m above the ground level (AGL) in 2006 and 18 m AGL in 2007 and 2008 using a Q7.1 net solar radiation instrument (REBS, Seattle, WA, USA), and a LI190 SB-L quantum sensor (Lincoln, NE, USA), respectively. Precipitation (P) was measured at 16 m AGL in 2006, and 18 m AGL in 2007 and 2008 using the TE525-L tipping-bucket rain gauge (Campbell Scientific, Inc., CSI, Logan, UT, USA). Air temperature and relative humidity were measured at four different heights (2 m, 6 m, 10 m, and 14 m AGL in 2006 and 5 m, 10 m, 15 m, and 20 m AGL in 2007 and 2008) using the HMP45C probe relative humidity and air temperature sensors (CSI).

The turbulent vertical fluxes of CO₂, water vapor, and latent and sensible heat were continuously measured with an open-path eddy covariance system (Li-7500, Lincoln, NE, USA and CSAT3, CSI). Both instruments were mounted 16 m AGL in 2006 and lifted to 18 m AGL in 2007 and 2008 to keep them above the roughness sublayer. The raw 10 Hz data were logged with a CR5000 data logger (CSI). The fluxes were calculated in the planar fit coordinate system (Leuning, 2004), and were corrected for density fluctuations (Webb et al., 1980) and storage in the canopy space. All calculations were done with the EC_PROCESSOR 2.1 software package (<http://www4.ncsu.edu/~anoorme/ECP/>). The NEE was calculated as the sum of the turbulent flux and the storage term. Canopy storage of CO₂ (F_s) was estimated from the half-hour change in the mean CO₂ concentration according to the approach of Hollinger et al. (1994):

$$F_s = \frac{\Delta c}{\Delta t} \cdot h \quad (1)$$

where Δc is the difference of CO₂ concentration between two consecutive measurements, Δt is the time interval between two consecutive measurements (set to 30 min for this study), and h is the measurement height.

Soil temperature profiles were measured at depths of 5 cm, 10 cm, and 20 cm by the TCAV107 soil temperature sensors (CSI). Volumetric soil water contents at 20 cm and 50 cm depth were measured by a CS616 water content reflectometer (CSI). All data were stored at 30-min intervals on a CR5000 data logger (CSI). Besides, a four-channel Multiplexer Automated Solution Monitoring System (Li-8150, Li-Cor, NE, USA) was used to measure soil respiration (SR) near the eddy flux tower in 2007 and 2008.

2.3. Data quality control and gap-filling

The data were screened and then evaluated for quality based on flux stationary (Foken et al., 2004), atmospheric stability (Hollinger et al., 2004), instrument quality flags and turbulent mixing as the key criteria. In addition, power failures resulted in the loss of 7%, 11%, and 5% of data in 2006, 2007, and 2008, respectively. The critical friction velocity values below which flux loss occurred were 0.18, 0.12 and 0.14 m s⁻¹ in 2006, 2007, and 2008, respectively. Altogether, 37–45% of the original EC flux data were rejected during the data quality control process, and gaps in 30-min NEE were filled using the dynamic parameter mechanistic models (Lloyd and Taylor, 1994; Noormets et al., 2007):

$$NEE = R_{10} e^{\frac{E_a}{R} \left(\frac{1}{T_{ref}} - \frac{1}{T_a} \right)} + \frac{\alpha Q_p A_{max}}{\alpha Q_p + A_{max}} \quad (2)$$

Table 1

Biophysical variables measured at the Daxing eddy flux tower site from 2006 to 2008. Day of the year – from 1 to 365, LAI = leaf area index, NEE = net ecosystem exchange, GEP = gross ecosystem productivity, ER = ecosystem respiration. The error estimates are standard deviation (SD) for average LAI during growing season and cumulative gap filling uncertainty across all gap filled periods for NEE.

		2006	2007	2008
Start of carbon uptake period (day of the year)	DOY	105	111	96
End of carbon uptake period (day of the year)	DOY	304	304	305
Carbon uptake period (CUP) (days)	DOY	200	194	210
Average LAI (growing season)	m ² m ⁻²	1.6 ± 0.4	1.8 ± 0.7	2.1 ± 0.6
NEE (g C m ⁻² year ⁻¹ for the growing season)	g C m ⁻² year ⁻¹	-591 ± 62	-641 ± 71	-929 ± 75
GEP (g C m ⁻² year ⁻¹ for the growing season)	g C m ⁻² year ⁻¹	1270	1233	1569
ER (g C m ⁻² year ⁻¹ for the growing season)	g C m ⁻² year ⁻¹	680	592	639

where R_{10} is reference respiration at a common temperature ($T_{ref} = 283.15 \text{ K} = 10 \text{ }^\circ\text{C}$), E_a is activation energy ($\text{kJ mol}^{-1} \text{ K}^{-1}$), R is universal gas constant ($8.3134 \text{ J mol}^{-1} \text{ K}^{-1}$), T_a is air temperature (K), α is apparent quantum yield ($\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ PAR}$), A_{max} is the maximum apparent photosynthetic capacity of canopy ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and Q_p is PAR ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$). R_{10} is a linear function of soil volumetric water content (VWC) during the growing season (Noormets et al., 2007, 2008):

$$R_{10} = a_0 + a_1 \cdot \text{VWC} \quad (3)$$

where a_0 is considered the same as R_{10} in moisture saturated conditions. a_1 is the unit change of R_{10} per unit change of VWC. The uncertainty in annual NEE caused by gap-filling was estimated according to Aurela et al. (2002) and Flanagan and Johnson (2005). During periods when gaps in micrometeorological data did not allow gap-filling with the mechanistic model (Eq. (2)), data were filled by a mean diurnal variation (MDV) method (Falge et al., 2001) using the mean values of monthly or weekly fixed MDV. The missing precipitation data were filled by the daily precipitation value measured at the Daxing Weather Station. We normalized GEP by monthly LAI when evaluating drought responses in different years because canopy closure has not yet occurred on the study site (Table 1).

2.4. Footprint analysis

The site was roughly square in shape with the tower located in the middle. The upwind distance from the plantation edge to the tower was approximately 450 m. We analyzed the footprint of the observed fluxes using wind data in 2008 and the model by Hsieh et al. (2000). The fetch was less than 500 m under unstable conditions and was ~2500 m for stable conditions (Fig. 1). Following quality screening according to criteria described above, very

stable and moderately stable situations accounted for 3% of the total screened data (0.5% of the daytime and 40% of the nighttime data). To evaluate the representativeness of the data, two data arrays that present the typical wind patterns in summer and winter 2008 were selected. We chose the data alignments and high atmospheric boundary layers (i.e., 2:00 pm each day). The results showed that the length of 80% of the footprint contribution in the dominant wind direction was 160 m in the summer and 180 m in the winter within the range of our measurement area.

2.5. Relative extractable water content and canopy conductance

Ecosystem drought responses were analyzed in terms of the availability of relative extractable water content (REW) in soil. Soil water stress was assumed to occur when the REW dropped below 0.4 (Granier et al., 1999, 2007; Bernier et al., 2002). Daily REW is calculated as:

$$\text{REW} = \frac{\text{VWC} - \text{VWC}_{\min}}{\text{VWC}_{\max} - \text{VWC}_{\min}} \quad (4)$$

where VWC_{\min} and VWC_{\max} are the minimum and maximum soil volumetric water content across the 3 years, respectively.

Canopy conductance, g_c (m s^{-1}), was estimated from the Penman–Monteith equation (Monteith, 1965):

$$g_c^{-1} = \left(\frac{\Delta}{\gamma} \cdot \frac{R_n}{\lambda E} - \frac{\Delta}{\gamma} - 1 \right) \cdot r_a + \frac{\rho C_p}{\gamma} \cdot \frac{\text{VPD}}{\lambda E} \quad (5)$$

where Δ is the slope of light saturation curve (kPa K^{-1}), γ is the psychrometric constant (kPa K^{-1}), R_n is the net radiation (W m^{-2}), λE is the latent heat flux (W m^{-2}), ρ is air density (kg m^{-3}), C_p is the specific heat capacity of air ($\text{kJ kg}^{-1} \text{ K}^{-1}$), VPD is the saturated vapor pressure deficit, and r_a is aerodynamic resistance (s m^{-1}) calculated as:

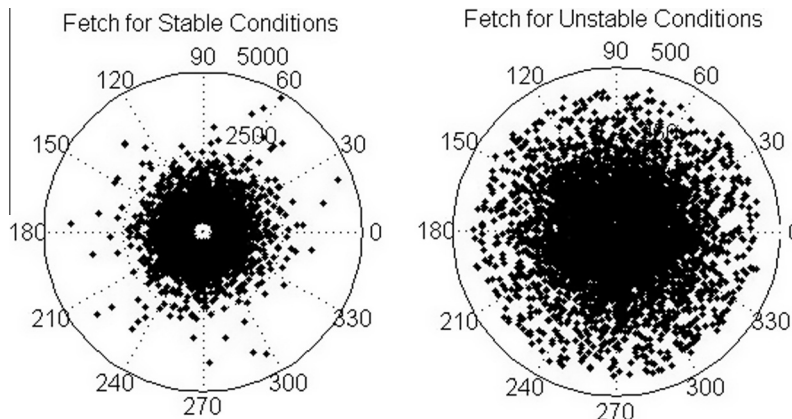


Fig. 1. Modeled fetch for stable conditions and unstable conditions in 2008. The tower is at the center of the circle. The radius of the left-hand circle (stable conditions) is 5000 m, and 80% of the 30-min data fall within a radius of 2500 m. The radius of the right-hand circle (unstable conditions) is 500 m that includes all of the 30-min data.

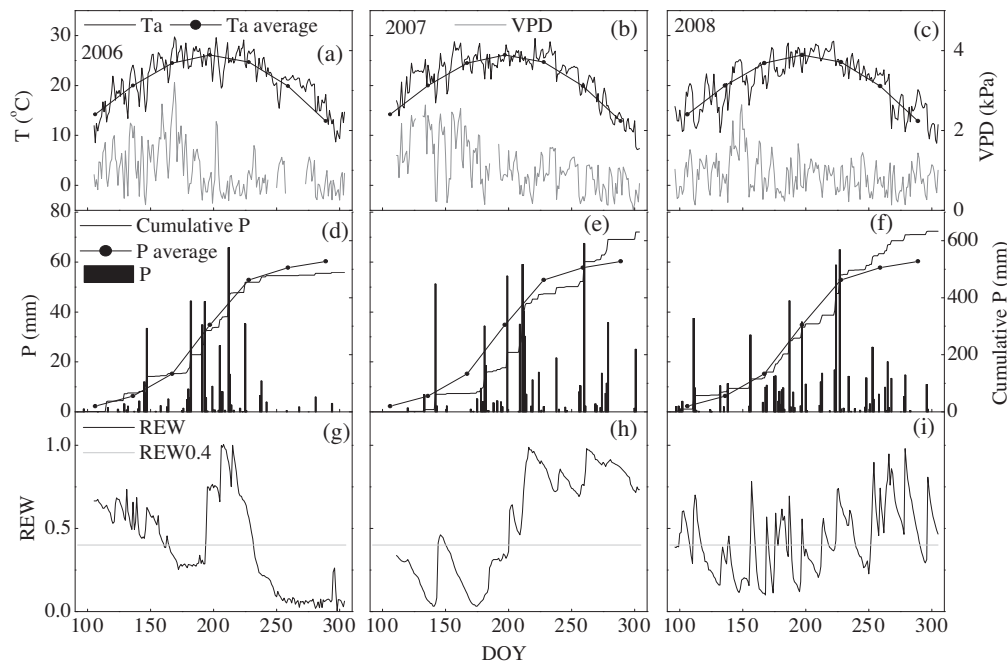


Fig. 2. Seasonal variations of (a–c) daily mean, monthly multi-average air temperature (T_a) and daily mean saturated vapor pressure deficit (VPD), (d–f) daily, annual cumulative, and monthly multi-average precipitation (P) and (g–i) relative extractable water content (REW) of the site from 2006 to 2008.

$$r_a = \frac{\ln[(z-d)/z_0] \cdot \ln[(z-d)/z_{0v}]}{\kappa^2 u} \quad (6)$$

where z is the height that wind speed (m) was measured, d is zero plane displacement (m), z_0 is momentum roughness length (m), z_{0v} is vapor pressure roughness length (m), κ is Karman constant, and u is mean horizontal wind speed ($m\ s^{-1}$). All g_c data were estimated under conditions with incoming solar radiation (R_n) $> 400\ W\ m^{-2}$, $VPD > 0.05\ kPa$, and $u > 0.5\ m\ s^{-1}$. The sensitivity of g_c to VPD was evaluated based on the reference conductance concept of Oren et al. (1999). However, since the slope of the g_c –VPD relationship was not representative at $VPD = 1\ kPa$, we reported the conductances and slopes at $VPD = 1.5\ kPa$ ($g_{c1.5}$).

2.6. Statistical analyses

Repeated measurement ANOVA (PROC MIXED, SAS 9.0) was used to compare the carbon fluxes and soil moisture among years, and ANOVA was used to compare the classes with different VWC. All analyses were carried out at $\alpha = 0.05$.

3. Results

3.1. Seasonal variation of environmental conditions

The daily mean air temperature (T_a) during growing seasons (i.e., April–October) for 2006, 2007, and 2008 ranged from 8.5 to 29.7 °C, 6.2 to 29.5 °C, and 8.4 to 28.8 °C, respectively. The maximum air temperature occurred in July in all 3 years. The monthly mean air temperature in October, 2006 and May, 2007 were significantly ($2 \pm 0.5\ ^\circ C$) higher than the other 2 years of the same months (i.e., 2006: $p = 0.018$; 2007: $p = 0.001$). There was also a significantly lower monthly mean air temperature in June, 2008 when compared with the other 2 years in June ($p < 0.001$, Fig. 2a–c).

In 2006, 433 mm of precipitation (P) occurred during the growing season of April to October, and additional irrigation was applied in April (35 mm) and May (21 mm). The total water supply

(i.e., precipitation plus irrigation) in 2006 was 489 mm, was 38 mm less than the long-term average of 527 mm (1990–2009), but over ~ 100 mm above the mean in 2007 and 2008 (631 mm and 632 mm, respectively). However, the timing of the water supply differed among the 3 years. The rainfall in late August and September of 2006 was nearly 110 mm and 180 mm less compared to the same period in 2007 and 2008, and 120 mm less than the long-term average. The rainfall was similar in 2007 and 2008, but was more evenly distributed in 2008. There was a drought period in 2007 from April to June when only 57 mm rainfall was received (Fig. 2d–f). A few large precipitation events ($P > 25\ mm\ d^{-1}$) after the drought (i.e., April–June) accounted for 85% of the accumulated rainfall during July, 2007. There was no flooding or runoff during these intensive rain events due to the high infiltration capacity of the sandy soil.

The VPD in the wet year 2008 ($0.87 \pm 0.3\ kPa$) was lower than those in 2006 and 2007 ($1.02 \pm 0.4\ kPa$). Higher T_a and lower P in April and May of 2007 led to higher VPD compared with the same time in 2006 and 2008 (Fig. 2a–c). Growing season VWC in the top 50 cm varied between 2.7% and 17.5%. Although there was only 2.9 mm rainfall in April of 2006 equal to about 15% and 5% of the same period in the long-term average and in 2008 ($p < 0.001$), severe drought (REW < 0.1) with a VWC below the wilting point (Tan et al., 2009) did not occur in response to less precipitation due to the additional irrigation. Severe drought was observed in late season of 2006, in spring in 2007 and not at all in 2008 (Fig. 2g–i).

3.2. Ecosystem carbon fluxes

Higher T_a in the spring of 2008 resulted in earlier bud-break, and longer growing season than in 2006 and 2007. The severe drought during early spring of 2007 delayed leaf emergence and led to the shortest growing season among the 3 years (Table 1).

The dynamics of NEE, ER, and GEP reflected the inter-annual differences in temperature and water availability (Fig. 3, Table 1). The mean daily NEE in the growing season was -3.0 ± 2.2 (mean \pm SD), -3.3 ± 1.8 , and $-4.4 \pm 3.1\ g\ C\ m^{-2}\ d^{-1}$ for 2006, 2007, and 2008,

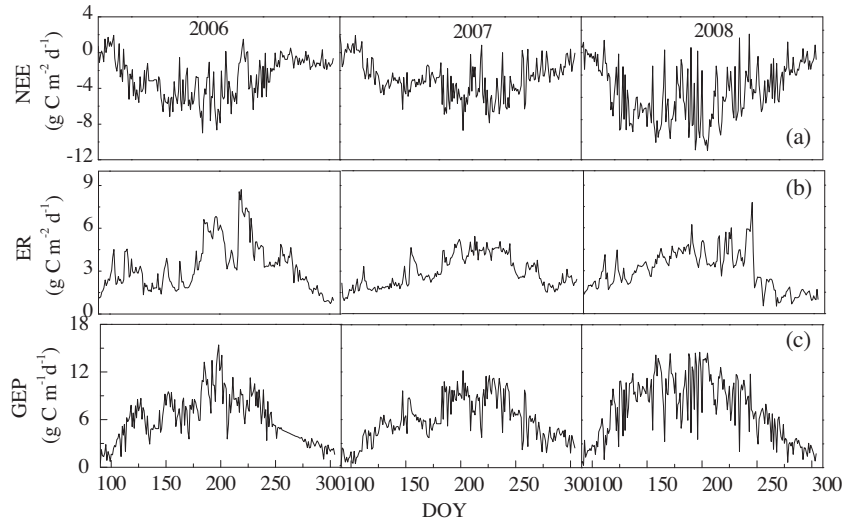


Fig. 3. Seasonal variations of: (a) daily net ecosystem exchange (NEE), (b) daily ecosystem respiration (ER), and (c) daily gross ecosystem productivity (GEP) during the growing season of the poplar plantation from 2006 to 2008.

respectively. The average daily GEP was 6.4 ± 2.9 , 6.4 ± 2.4 , and $7.5 \pm 3.8 \text{ g C m}^{-2} \text{ d}^{-1}$ for 2006, 2007, and 2008, respectively. The mean daily growing season ER was 3.4 ± 1.2 , 3.1 ± 1.1 , and $3.0 \pm 1.4 \text{ g C m}^{-2} \text{ d}^{-1}$ in 2006, 2007, and 2008, respectively. All of these differences were statistically significant among 3 years ($p < 0.001$). Carbon uptake increased abruptly during leaf emergence in April and decreased rapidly in late August. Daily GEP and NEE peaked in July with rates of 15, 12, and $15 \text{ g C m}^{-2} \text{ d}^{-1}$ and -9 , -9 , and $-11 \text{ g C m}^{-2} \text{ d}^{-1}$ in 2006, 2007, and 2008, respectively. However, the ER of 9, 5, and $8 \text{ g C m}^{-2} \text{ d}^{-1}$ was highest in August during each of 3 years. The sums of GEP, ER, and NEE in the growing seasons from 2006 to 2008 are given in Table 1 and Fig. 3. The largest carbon sink (i.e., $\text{NEE} = -929 \pm 75 \text{ g C m}^{-2}$, $\text{sum} \pm \text{gap-filling uncertainty}$) and the highest GEP (i.e., 1569 g C m^{-2}) occurred in 2008, with both observed following higher than average significant periods of precipitation.

3.3. Effects of soil water on carbon flux

There were significant differences ($p < 0.001$) in seasonal and inter-annual LAI-normalized GEP (i.e., GEP:LAI) among the 3 years, consistent with differences in VWC. The LAI-normalized GEP during the spring drought in 2007 was 11% and 20% less ($p < 0.001$) than that during the same period in 2006 and 2008, respectively. The late-season drought in 2006 similarly resulted in 20% less ($p < 0.001$) GEP:LAI than during the same period in 2007 and 2008 (Fig. 4a). In addition, the light-saturated photosynthesis (A_{max}) was 26% and 47% lower during the spring drought in 2007 than that in 2006 and 2008 during the same period. A_{max} in the dry period of 2006 was 12% and 7% less than that in the same period of 2007 and 2008, respectively. The lowest A_{max} and ecosystem quantum (α) value during the growing season occurred in 2007 (Table 2).

Seasonal and inter-annual differences of reference respiration (R_{10}) were attributable to differences in water conditions, with 8% and 14% lower R_{10} during spring drought in 2007 than it was during the same period in 2006 and 2008, respectively (Fig. 4b). Furthermore, the seasonal variations of ER/GEP ratio were the largest during the droughts of 2006 and 2007. Although both GEP and ER decreased under drought, the increase in ER/GEP ratio indicates that water limitation suppressed carbon assimilation more than carbon release (Fig. 4c). It appears that the net effect of declining GEP and ER under drought led to lower net ecosystem production

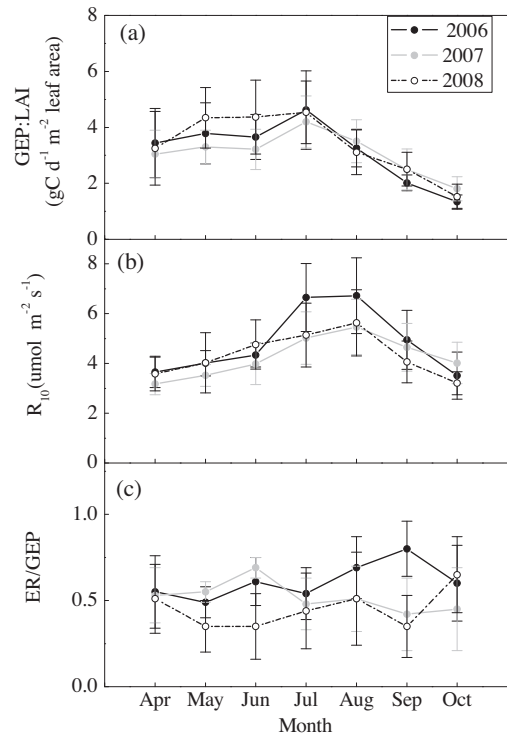


Fig. 4. Seasonal variation of: (a) monthly mean LAI-normalized gross ecosystem productivity (GEP:LAI), (b) monthly mean reference respiration (R_{10}), and (c) monthly mean ecosystem respiration (ER): gross ecosystem productivity (GEP) during the growing seasons of the poplar plantation from 2006 to 2008, the error bars represent the standard deviation (SD).

($\text{NEP} = -\text{NEE}$). The sensitivity of GEP:LAI to PAR under different REWs varied among the 3 years (Fig. 5a–c). Low REW significantly decreased the relationship between GEP:LAI and PAR in 2006 and 2007, and this impact became more pronounced as PAR increased (Fig. 5a and b). However, in the wetter year of 2008, there was no significant effect of REW on the relationship between GEP:LAI and PAR (Fig. 5c). The slope and compensation point of the daily GEP:LAI–PAR relationship was the greatest in 2008, and the least during 2006 under drought. Additionally, the GEP:LAI ratio was less in 2006 than that in 2007 when there was a severe drought (Fig. 5d–f).

Table 2
Estimates of light response parameters modeled using Eq. (2) (α , apparent quantum yield, $\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{PAR}$; A_{max} , maximum apparent photosynthetic capacity of canopy, $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; R_d , daytime ecosystem respiration, $\mu\text{mol C m}^{-2} \text{s}^{-1}$) and associated standard errors (SE) based on the 30-min CO_2 flux data. R^2 is the determination coefficient and N is the number of 30-min data periods.

Year	Period	α	SE	A_{max}	SE	R_d	SE	R^2	N
2006	April–June	0.078	0.057	22.46	1.99	7.18	2.20	0.37	1857
	July–August	0.055	0.022	42.95	1.49	9.65	1.72	0.65	1232
	September	0.038	0.049	19.73	2.08	6.23	1.70	0.39	180
	Growing season	0.064	0.044	28.84	2.84	7.85	2.12	0.37	3269
2007	April–June	0.067	0.086	16.59	2.64	5.05	2.57	0.19	1812
	July–August	0.045	0.018	36.51	1.74	7.10	1.42	0.59	1230
	September	0.022	0.006	32.93	2.59	3.31	0.55	0.65	650
	Growing season	0.052	0.050	25.96	3.33	6.74	2.00	0.30	3692
2008	April–June	0.085	0.025	31.33	1.14	7.31	1.30	0.57	1918
	July–August	0.065	0.013	45.31	1.88	7.68	1.13	0.68	1334
	September	0.049	0.013	21.16	1.02	3.53	0.73	0.51	634
	Growing season	0.073	0.019	34.29	2.37	6.80	1.15	0.50	3886

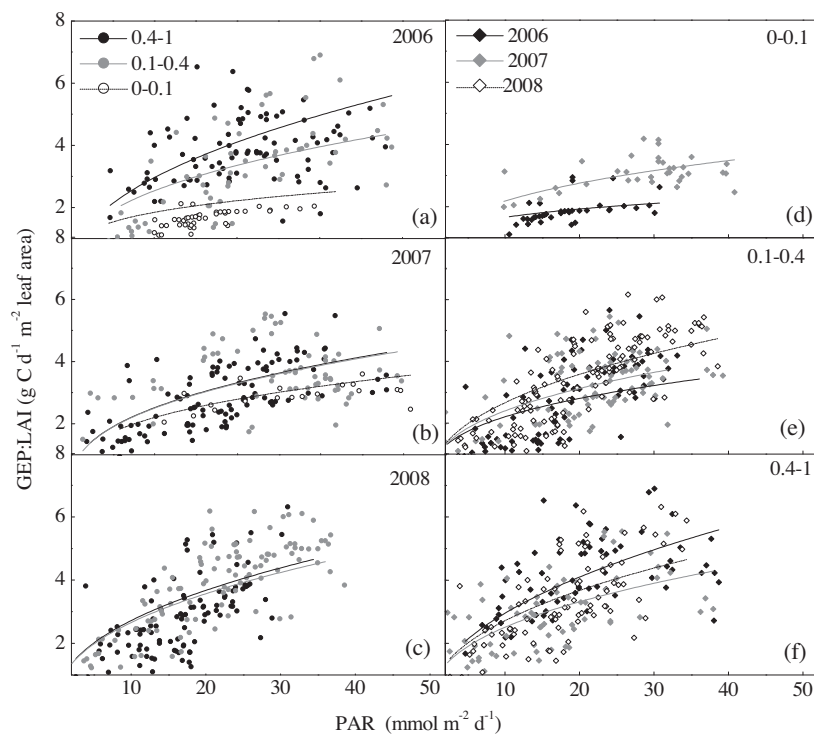


Fig. 5. The response of LAI-normalized gross ecosystem productivity (GEP:LAI) to photosynthetically active radiation (PAR) under different relative extractable water content (REW) during the growing seasons of 2006–2008.

3.4. Variability of g_c with VPD

Canopy conductance (g_c) ranged from 0.5 to 45 mm s^{-1} and declined exponentially with VPD at $\text{VPD} < 1.5 \text{ kPa}$ (Fig. 6a). For $\text{VPD} > 1.5 \text{ kPa}$, stomatal closure limited water loss, and g_c was less than 10 mm s^{-1} (Fig. 6a). Canopy conductance at $\text{VPD} = 1.5 \text{ kPa}$ ($g_{c1.5}$) which is a moisture indicator, was suppressed from April to June of 2007, as well as in September 2006 (Fig. 6b) due to lower soil water content (Fig. 7). Consequently, NEP was also low during this drought period.

4. Discussion

4.1. Influence of drought on carbon exchange

Daily PAR accounted for 34%, 38%, and 74% of seasonal variations in GEP:LAI in 2006, 2007, and 2008, respectively (Fig. 5). These results indicated that PAR had less influence on the changes

in carbon fluxes in 2006 and 2007 compared with 2008. Therefore, PAR was a major (but not the only) determinant in the variations of carbon flux. Atmospheric temperature and water conditions may also control carbon exchange (Aubinet et al., 2001). The low sensitivity of the compensation point to PAR was found during the dry periods (Fig. 5a–c) due to the limitation of high VPD and low soil water content. Both VPD and soil water impact stomatal closure, and thus potential GEP (Carrara et al., 2004). This was also supported in current study by measurements of suppressed g_c under high VPD and lower $g_{c1.5}$ under drought conditions (Figs. 6a and 7).

Differences in ER between wet and dry periods were governed by both temperature and soil moisture conditions. The decomposition of organic matter, autotrophic respiration, coarse woody debris decomposition, and even leaf or wood respiration were reduced under dry soil conditions (Davidson et al., 2000; Epron et al., 2004; Salimon et al., 2004; Chambers et al., 2001; Cavaleri et al., 2006). Moreover, ER and SR could be limited by drought during the growing season (Yuste et al., 2003; Jassal et al., 2007). The mean annual

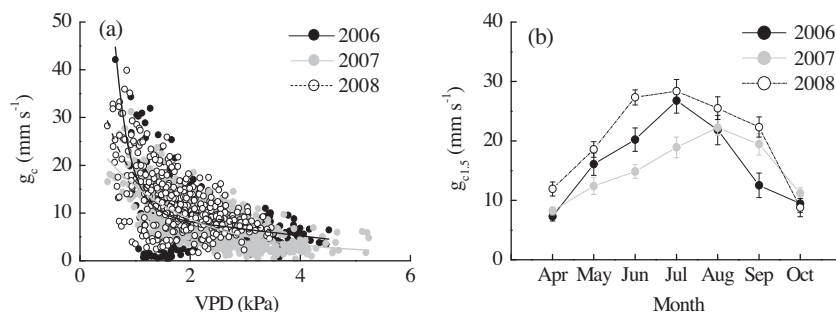


Fig. 6. (a) The relationship between canopy conductance (g_c) and vapor pressure deficit (VPD) and (b) the seasonal dynamics of canopy conductance at VPD = 1.5 kPa ($g_{c1.5}$), the error bars represent the standard deviation (SD).

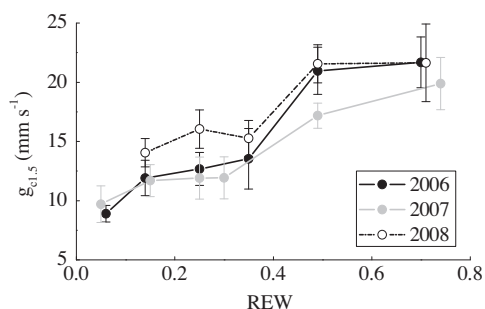


Fig. 7. Variation of canopy conductance at VPD = 1.5 kPa ($g_{c1.5}$) under different relative extractable water content (REW) classes, the error bars represent the standard deviation (SD).

SR/ER ratio was 0.68 and 0.73 for 2007 and 2008, respectively. These values are similar to 0.69 recorded in European Forests (Janssens et al., 2001) and 0.75 reported by Law et al. (2002). In addition, the impact of soil moisture on SR and the sensitivity of SR to temperature (i.e., Q_{10}) at this site were studied by Tan et al. (2009) who reported that the soil water content for optimum SR is between wilting point (WP, VWC = 6%, REW = 0.2) and the water content of rupture of capillary (WRC, VWC = 11%, REW = 0.6, 80% of field capacity). They also observed that the Q_{10} was lower in both dry and very wet soil conditions. The negative impact of dry soil conditions on Q_{10} was also reported in other studies (Davidson et al., 2000; Yuste et al., 2003; Palmroth et al., 2005). Reichstein et al. (2002) suggested that the activities of roots and microorganisms are inhibited by dry soil, and may limit soil respiration.

The limitation of NEP under drought was caused primarily by the drought induced suppression of GEP, whereas the decrease in ER had a minimal effect (Fig. 4c). Soil water had a greater influence on GEP than on ER (Yuan et al., 2010), possibly because the canopy conductance in poplar trees was very sensitive to soil moisture (Cai et al., 2011). However, a different result was found in mature aspen forest in southern Saskatchewan, where severe drought suppressed both ER and GEP to a similar extent and therefore NEE was relatively unaffected by severe drought (Barr et al., 2007).

4.2. Annual carbon exchange

Some studies showed that annual ecosystem productivity on a global scale is highly correlated with mean annual temperature and precipitation (O'Neil and DeAngelis, 1981; Sun et al., 2011b), while other studies suggest that annual GEP is more sensitive to annual temperature than to soil water availability at a given site (Law et al., 2002; Xu et al., 2011). In our study, upon accounting for inter-year increases in LAI in the aggrading poplar stand, the main source of inter-annual variability in GEP was water availability, with the timing of drought as an additional modifying factor.

Cumulative GEP in 2007 was the lowest among the 3 years due to the severe drought in spring despite the similar total annual precipitation being equal to 2008 values (Fig. 4a, Table 1). There were five large precipitation events in July 2007 following the severe drought. Despite the heavy rainfall, approximately 35% of precipitation was lost due to deep seepage and 50% of the precipitation was lost as evapotranspiration (ET) during this period (Zhang et al., in preparation). This indicated that, despite the heavy rainfall, infiltrated rain water would not be fully used by vegetation because of the low soil water holding capacity. Although the rainfall in April of 2006 was very low, there was no severe drought and significant limitation on GEP ($p > 0.05$) (Table 2) as the irrigation reduced negative drought impacts on carbon sequestration.

Furthermore, the causes of inter-annual variation of ER are not consistent among studies. In some cases, ER has been found to vary significantly with annual rainfall (Law et al., 2000; Pilegaard et al., 2001; Morgenstern et al., 2004), whereas in other studies ER has been relatively invariant despite significant inter-annual climate variations (Black et al., 2000; Arain et al., 2002; Barr et al., 2002; Griffis et al., 2003). In our study, ER was the lowest in 2007 likely due to the severe drought in spring. The highest ER occurred in 2006 (i.e., the driest year), indicating that the impact of water limitation on inter-annual changes of ER was overridden by some other factor (Fig. 4b, Table 1). The annual ER was the highest among the 3 years in 2006 due in part to large ER in July and August. The high annual ER coincided with tilling which promoted permeability and decomposition of dead plant material, both above and below ground, thus inducing the higher SR (Zhang et al., 2008; Yu et al., 2012). Therefore, at this site, it is evident that inter-annual variation in ER was impacted by human disturbance as well as by natural variations in temperature and soil moisture.

In summary, the poplar plantation in this sandy soil in northern China was a strong carbon sink fixing 590–930 $\text{g C m}^{-2} \text{ year}^{-1}$ in the growing season. Carbon accumulation was 30–35% higher in a year without a significant drought. Although some studies concluded that spring temperature was the primary climatic control of the inter-annual variability of NEE (Black et al., 2000; Barr and Barbe, 2004), significant drought and human activities during the growing season were the primary factors in our study.

4.3. Comparison with other ecosystems

Compared with another poplar plantation of similar age and soil type, GEP is similar during the growing season but NEP is 20% higher, largely because ER is 25% lower in our study (Migliavacca et al., 2009). The study by Cai et al. (2011) reported that a 5 year old hybrid poplar plantation had 30% lower annual ER, 65% lower annual GEP, and 98% lower NEP than our values. Barr et al. (2007) reported that in a 90+ year old boreal aspen forest, annual ER that was 70% higher, a GEP that was 7% lower, and a NEP that was 76% lower compared to our study.

Compared with other temperate and temperate-humid deciduous forests, GEP from our study (i.e., $1452 \pm 102 \text{ g C m}^{-2} \text{ year}^{-1}$, mean \pm SD) was very comparable to the range of temperate deciduous forests ($1508 \text{ g C m}^{-2} \text{ year}^{-1}$, Wilson and Baldocchi, 2000; Wilson et al., 2000; $1360 \text{ g C m}^{-2} \text{ year}^{-1}$, Schmid et al., 2003; $1375 \pm 56 \text{ g C m}^{-2} \text{ year}^{-1}$, Luysaert et al., 2007) but far exceeded the values reported for Harvard Forest ($987 \text{ g C m}^{-2} \text{ year}^{-1}$) (Goulden et al., 1996; Law et al., 2002). The normal rotation length of a poplar plantation is approximately 15 years, and the current plantation is approaching its peak productivity (i.e., GEP). However, ER in our studies showed a lower value than that in the other ecosystems (Luysaert et al., 2007; Law et al., 2002) except deciduous forest in Harvard Forest (Goulden et al., 1996; Law et al., 2002). The relatively low ER values in this study may be partly caused by the lack of litter and organic matter accumulation. Overall, the 10 year old poplar plantation at our site, regardless of the dry conditions in the summer and the scarce and unevenly distributed rainfall, was a strong carbon sink, primarily due to relatively low ER.

The inter-annual variation of $\pm 183 \text{ g C m}^{-2} \text{ year}^{-1}$ in annual NEE of the plantation was larger than that of measure over other temperate deciduous forests (i.e., $\pm 38 \text{ g C m}^{-2} \text{ year}^{-1}$, Barford et al., 2001; $\pm 23 \text{ g C m}^{-2} \text{ year}^{-1}$, Schmid et al., 2003; $\pm 94 \text{ g C m}^{-2} \text{ year}^{-1}$, Barr et al., 2007; $\pm 38 \text{ g C m}^{-2} \text{ year}^{-1}$, Luysaert et al., 2007; $\pm 63 \text{ g C m}^{-2} \text{ year}^{-1}$, Migliavacca et al., 2009). The greater inter-annual variability of NEE may be attributed to the fast growing nature of poplar plantations. In another words, these trees were more sensitive to environmental and human disturbances than other slow growing forests.

5. Conclusions

Poplar plantations have a large potential for carbon sequestration due to their high productivity. However, they may require more water to maintain high growth rates in the region of the study area. At our site, the GEP of the poplar plantation was more sensitive to soil moisture stress than ER, and thus NEP was suppressed during periodic droughts. The timing of severe drought significantly impacted annual GEP. The severe drought during canopy development induced a lasting reduction in carbon exchange throughout the growing season, while droughts at the end of growing season did not result in such a limitation. In addition, relatively high inter-annual variations of carbon exchange indicate that fast growing poplar plantations in the region are sensitive to the changes in environmental conditions and human activities, such as rainfall patterns and irrigation. Therefore, regional planning that uses poplars as the key species in northern China should consider the potential impacts of climate change as well as land management operations such as irrigation and tillage.

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References

- Amthor, J.S., Baldocchi, D.D., 2001. Terrestrial higher plant respiration and net primary production. In: Roy, B.S.J., Mooney, H.A. (Eds.), *Terrestrial Global Productivity*. Academic Press, San Diego, pp. 33–59.
- Arain, M.A., Black, T.A., Barr, A.G., Jarvis, P.G., Massheder, J.M., Verseghy, D.L., Nesic, Z., 2002. Effects of seasonal and interannual climate variability on net ecosystem productivity of boreal deciduous and conifer forests. *Canadian Journal of Forest Research* 32, 878–891.
- Aubinet, M., Chermanne, B., Vandenhaute, M., Longdoz, B., Yernaux, M., Laitat, E., 2001. Long-term carbon dioxide exchange above a mixed forest in the Belgian Ardennes. *Agriculture and Forest Meteorology* 108, 293–315.
- Aurela, M., Laurila, T., Tuovinen, J.P., 2002. Annual CO₂ balance of a subarctic fen in northern Europe: importance of the wintertime efflux. *Journal of Geophysical Research-Atmospheres* 107, 4607.
- Baldocchi, D., 2008. 'Breathing' of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany* 56, 1–26.
- Barford, C.C., Wofsy, S.C., Goulden, M.L., Munger, J.W., Pyle, E.H., Urbanski, S.P., Hutyrá, L., Saleska, S.R., Fitzjarrald, D., Moore, K., 2001. Factors controlling long- and short-term sequestration of atmospheric CO₂ in a mid-latitude forest. *Science* 294, 1688–1691.
- Barr, A.E., Barbe, M.F., 2004. Inflammation reduces physiological tissue tolerance in the development of work related musculoskeletal disorders. *Journal of Electromyography and Kinesiology* 14, 77–85.
- Barr, A.G., Black, T.A., Hogg, E.H., Griffis, T.J., Morgenstern, K., Kljun, N., Theede, A., Nesic, Z., 2007. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. *Global Change Biology* 13, 561–576.
- Barr, A.G., Griffin, T.J., Black, T.A., Lee, X., Staebler, R.M., Fuentes, J.D., Chen, Z., Morgenstern, K., 2002. Comparing the carbon budgets of boreal and temperate deciduous forest stands. *Canadian Journal of Forest Research* 32, 813–822.
- Bernier, P.Y., Bréda, N., Granier, A., Raulier, F., Mathieu, F., 2002. Validation of a canopy gas exchange model and derivation of a soil water modifier for transpiration for sugar maple (*Acer saccharum* Marsh.) using sap flow density measurements. *Forest Ecology and Management* 163, 185–196.
- Black, T.A., Chen, W.J., Barr, A.G., Arain, M.A., Chen, Z., Nesic, Z., Hogg, E.H., Neumann, H.H., Yang, P.C., 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters* 27, 1271–1274.
- Bonal, D., Bosc, A., Ponton, S., Goret, J.Y., Burban, B.I.T., Gross, P., Bonnefond, J.M., Elbers, J., Longdoz, B., Epron, D., Guehl, J.M., Granier, A., 2008. Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana. *Global Change Biology* 14, 1917–1933.
- Cai, T., Price, D.T., Orchansky, A.L., Thomas, B.R., 2011. Carbon, water, and energy exchanges of a hybrid poplar plantation during the first five years following planting. *Ecosystems* 14, 658–671.
- Carrara, A., Janssens, I.A., Yuste, J.C., Ceulemans, R., 2004. Seasonal changes in photosynthesis, respiration and NEE of a mixed temperate forest. *Agricultural and Forest Meteorology* 126, 15–31.
- Cavaleri, M.A., Oberbauer, S.F., Ryan, M.G., 2006. Wood CO₂ efflux in a primary tropical rain forest. *Global Change Biology* 12, 2442–2458.
- Chambers, J.Q., Schimel, J.P., Nobre, A.D., 2001. Respiration from coarse wood litter in central Amazon forests. *Biogeochemistry* 52, 115–131.
- Chinese Forestry Society, National Poplar Commission, 2003. Forest resource, timber production and popular culture in China. In: 1st International Conference on the Future of Poplar, Rome. <<http://www.fao.org/forestry/site/20587/en/>>.
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A., Friedlingstein, P., Gobron, N., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krininger, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437, 529–533.
- Davidson, E.A., Verchot, L.V., Cattânio, J.H., Ackerman, I.L., Carvalho, J., 2000. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry* 48, 53–69.
- Epron, D., Nouvellon, Y., Rouspard, O., Mouvondy, W., Mabiala, A., Saint-Andre, L., Joffre, R., Jourdan, C., Bonnefond, J.M., Berbigier, P., Hamel, O., 2004. Spatial and temporal variations of soil respiration in a Eucalyptus plantation in Congo. *Forest Ecology and Management* 202, 149–160.
- Ewers, B.E., Mackay, D.S., Samanta, S., 2007. Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species. *Tree Physiology* 27, 11–24.
- Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Doman, H., Granier, A., Gross, P., Grunwald, T., Hollinger, D., Jensen, N.O., Katul, G., Keronen, P., Kowalski, A., Lai, C.T., Law, B.E., Meyers, T., Moncrieff, J., Moors, E., Munger, J.W., Pilegaard, K., Rannik, U., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology* 107, 43–69.
- Flanagan, L.B., Johnson, B.G., 2005. Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agricultural and Forest Meteorology* 130, 237–253.

- Foken, T., Göckede, M., Mauder, M., Mahrt, L., Amiro, B.D., Munger, J.W., 2004. Post-field data quality control. In: Lee, X., Massman, W.J., Law, B. (Eds.), *Handbook of Micrometeorology: A Guide for Surface Flux Measurement and Analysis*. Kluwer, Dordrecht, pp. 181–208.
- Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C., Wofsy, S.C., 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* 271, 1576–1578.
- Granier, A., Bréda, N., Biron, P., Villette, S., 1999. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecological Modelling* 116, 269–283.
- Granier, A., Ceschia, E., Damesin, C., Dufrene, E., Epron, D., Gross, P., Lebaube, S., Ledantec, V., Le Goff, N., Lemoine, D., Lucot, E., Ottorini, J.M., Pontailleur, J.Y., Saugier, B., 2000. The carbon balance of a young beech forest. *Functional Ecology* 14, 312–325.
- Granier, A., Reichstein, M., Breda, N., Janssens, I.A., Falge, E., Ciais, P., Grunwald, T., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Knohl, A., Kostner, B., Lagergren, F., Lindroth, A., Longdoz, B., Loustau, D., Mateus, J., Montagnani, L., Nys, C., Moors, E., Papale, D., Peiffer, M., Pilegaard, K., Pita, G., Pumpanen, J., Rambal, S., Rebmann, C., Rodrigues, A., Seufert, G., Tenhunen, J., Vesala, T., Wang, Q., 2007. Evidence of soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology* 143, 123–145.
- Griffis, T.J., Black, T.A., Morgenstern, K., Barr, A.G., Nescic, Z., Drewitt, G.B., Gaumont-Guay, D., McCaughey, J.H., 2003. Ecophysiological controls on the carbon balances of three southern boreal forests. *Agriculture and Forest Meteorology* 117, 53–71.
- Grünzweig, J.M., Lin, T., Rotenberg, E., Schwartz, A., Yakir, D., 2003. Carbon sequestration in arid-land forest. *Global Change Biology* 9, 791–799.
- Hollinger, D.Y., Aber, J., Dail, B., Davidson, E.A., Goltz, S.M., Hughes, H., Leclerc, M.Y., Lee, J.T., Richardson, A.D., Rodrigues, C., Scott, N.A., Achuatavariar, D., Walsh, J., 2004. Spatial and temporal variability in forest-atmosphere CO₂ exchange. *Global Change Biology* 10, 1689–1706.
- Hollinger, D.Y., Kelliher, F., Byers, J.N., Hunt, J.E., McSeveny, T., Weir, P., 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* 75, 134–150.
- Hsieh, C.I., Katul, G., Chi, T.W., 2000. An approximate analytical model for footprint estimation of scalar fluxes in thermally stratified atmospheric flows. *Advances in Water Resources* 23, 765–772.
- Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E., Smith, S.D., Tissue, D.T., Zak, J.C., Welton, J.F., Pockman, W.T., Sala, O.E., Haddad, B.M., Harte, J., Koch, G.W., Swinney, S., Small, E.E., Williams, D.G., 2004. Convergence across biomes to a common rain-use efficiency. *Nature* 419, 651–654.
- Jackson, R.B., Jobbágy, E.G., Avissar, R., Roy, S.B., Barrett, D.J., Cook, C.W., Farley, K.A., Maitre, D.C., McCarl, B.A., Murray, B.C., 2005. Trading water for carbon with biological carbon sequestration. *Science* 310, 1944–1947.
- Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltechev, S., Clement, R., Guemundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Shulze, E.D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7, 269–278.
- Jassal, R.S., Black, T.A., Cai, T., Morgenstern, K., Li, Z., Gaumont-Guay, D., Nescic, Z., 2007. Components of ecosystem respiration and an estimate of net primary productivity of an intermediate-aged Douglas-fir stand. *Agricultural and Forest Meteorology* 144, 44–57.
- Kljun, N., Black, T.A., Griffis, T.J., Barr, A.G., Gaumont-Guay, D., Morgenstern, K., McCaughey, J.H., Nescic, Z., 2006. Response of net ecosystem productivity of three boreal forest stands to drought. *Ecosystems* 9, 1128–1144.
- Law, B.E., Falge, E., Gu, L., Baldocchi, D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A.J., Falk, M., Fuentes, J.D., Goldstein, A., Granier, A., Grelle, A., Hollinger, D., Janssens, I.A., Jarvis, P., Jensen, N.O., Katul, G., Mahli, Y., Matteucci, G., Meyers, T., Monson, R., Munger, W., Oechel, W., Olson, R., Pilegaard, K., Paw, U.K.T., Thorgeirsson, H., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology* 113, 97–120.
- Law, B.E., Williams, M., Anthoni, P.M., Baldocchi, D., Unsworth, M.H., 2000. Measuring and modelling seasonal variation of carbon dioxide and water vapour exchange of a *Pinus ponderosa* forest subject to soil water deficit. *Global Change Biology* 6, 613–630.
- Le Dantec, V., Dufrene, E., Saugier, B., 2000. Interannual and spatial variation in maximum leaf area index of temperate deciduous stands. *Forest Ecology and Management* 134, 71–81.
- Leuning, R., 2004. Measurements of trace gas fluxes in the atmosphere using eddy covariance. WPL corrections revisited. In: Lee, X., Massman, W., Law, B. (Eds.), *Handbook of Micrometeorology: A Guide for Surface Flux Measurement and Analysis*. Kluwer Academic Publisher, Dordrecht, pp. 119–132.
- Liu, C., Zhang, Z., Sun, G., Zhu, J., Zha, T., Shen, L., Chen, J., Fang, X., Chen, J., 2009. Quantifying evapotranspiration and the biophysical regulations of a poplar plantation assessed by eddy covariance and sap flow methods. *Journal of Plant Ecology* 33, 706–718.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8, 315–323.
- Luyssaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichsteins, M., Papale, D., Piao, S.L., Schulzes, E.D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beers, C., Bernhoffer, C., Black, K.G., Bonal, D., Bonnefond, J.M., Chambers, J., Ciais, P., Cook, B., Davis, K.J., Dolman, A.J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grunwald, T., Guidolotti, G., Hanson, P.J., Harding, R., Hollinger, D.Y., Hutyrá, L.R., Kolar, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B.E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J.W., Nikinmaa, E., Ollinger, S.V., Pita, G., Rebmann, C., Rouspard, O., Saigusa, N., Sanz, M.J., Seufert, G., Sierra, C., Smith, M.L., Tang, J., Valentini, R., Vesala, T., Janssens, I.A., 2007. CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology* 13, 2509–2537.
- Meir, P., Brando, P.M., Nepstad, D., Vasconcelos, S., Costa, A., Davidson, E., Almeida, S., Fisher, R.A., Sotta, E.D., Zarin, D., Cardinot, G., 2009. The effects of drought on Amazonian rain forests. In: Keller, M.B., Gash, M., Dias, P.S.J. (Eds.), *Amazonian and Global Change*. Geophysical Monograph Series. American Geophysical Union, USA, pp. 429–449.
- Meir, P., Metcalfe, D.B., Costa, A.C.L., Fisher, R.A., 2008. The fate of assimilated carbon during drought: impacts on respiration in Amazon rainforests. *Philosophical Transactions of the Royal Society B – Biological Sciences* 363, 1849–1855.
- Meir, P., Woodward, F.I., 2010. Amazonian rain forests and drought: response and vulnerability. *New Phytologist* 187, 553–557.
- Migliavacca, M., Meroni, M., Manca, G., Matteucci, G., Montagnani, L., Grassi, G., Zenone, T., Teobaldelli, M., Godec, L., Colombo, R., Seufert, G., 2009. Seasonal and interannual patterns of carbon and water fluxes of a poplar plantation under peculiar eco-climatic conditions. *Agricultural and Forest Meteorology* 149, 1460–1476.
- Monteith, J.L., 1965. Evaporation and environment. *Symposia of the Society for Experimental Biology* 19, 205–234.
- Morgenstern, K., Black, T.A., Humphreys, E.R., Griffis, T.J., Drewitt, G.B., Cai, T., Nescic, Z., Spittlehouse, D.L., Livingston, N.J., 2004. Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño La Niña cycle. *Agricultural and Forest Meteorology* 123, 201–219.
- Noormets, A., Chen, J., Crow, T.R., 2007. Age-dependent changes in ecosystem carbon fluxes in managed forests in northern Wisconsin, USA. *Ecosystems* 10, 187–203.
- Noormets, A., Desai, A., Cook, B.D., Ricciuto, D.M., Euskirchen, E.S., Davis, K., Bolstad, P., Schmid, H.P., Vogel, C.S., Carey, E.V., Su, H.B., Chen, J.Q., 2008. Moisture sensitivity of ecosystem respiration: comparison of 14 forest ecosystems in the Upper Great Lakes Region, USA. *Agricultural and Forest Meteorology* 148, 216–230.
- Noormets, A., Gavazzi, M.J., McNulty, S.G., Domec, J.C., Sun, G., King, J.S., Chen, J.Q., 2010. Response of carbon fluxes to drought in a coastal plain loblolly pine forest. *Global Change Biology* 16, 272–287.
- O'Neil, R.V., DeAngelis, D.L., 1981. Comparative productivity and biomass relationships of forest ecosystem. In: Reichle, D.E. (Ed.), *Dynamic Properties of Forest Ecosystems*. Cambridge University Press, Cambridge, UK, pp. 411–450.
- Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K., 1999. Survey and synthesis of intra- and inter-specific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell and Environment* 22, 1515–1526.
- Palmroth, S., Maier, C.A., McCarthy, H.R., Oishi, A.C., Kim, H.S., Johnsen, K.H., Katul, G.G., Oren, R., 2005. Contrasting responses to drought of forest floor CO₂ efflux in a loblolly pine plantation and a nearby Oak-Hickory forest. *Global Change Biology* 11, 421–434.
- Pilegaard, K., Hummelshøj, P., Jensen, N.O., Chenc, Z., 2001. Two years of continuous CO₂ eddy-flux measurements over a Danish beech forest. *Agricultural and Forest Meteorology* 107, 29–41.
- Reichstein, M., Tenhunen, J.D., Rouspard, O., Ourcival, J.M., Rambal, S., Dore, S., Valentini, R., 2002. Ecosystem respiration in two Mediterranean evergreen Holm Oak forests: drought effects and decomposition dynamics. *Function Ecology* 16, 27–39.
- Reichstein, M., Tenhunen, J., Rouspard, O., Ourcival, J.M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G., Valentini, R., 2003. Inverse modeling of seasonal drought effects on canopy CO₂/H₂O exchange in three Mediterranean ecosystems. *Journal of Geophysical Research-Atmospheres* 108, 4726.
- Salimon, C.I., Davidson, E., Victoria, R., Melo, A., 2004. CO₂ flux from soil in pastures and forests in Southwestern Amazonia. *Global Change Biology* 10, 833–843.
- Schmid, H.P., Su, H.B., Vogel, C.S., Curtis, P.S., 2003. Ecosystem-atmosphere exchange of carbon dioxide over a mixed hardwood forest in northern lower Michigan. *Journal of Geophysical Research-Atmospheres* 108, 4417.
- Scurlcock, J.M.O., Olson, R.J., 2002. Terrestrial net primary productivity – a brief history and a new worldwide database. *Environmental Reviewers* 10, 91–109.
- Sun, G., Alstad, K., Chen, J., Chen, S., Ford, C.R., Lin, G., Liu, C., Lu, N., McNulty, S.G., Miao, H., Noormets, A., Vose, J.M., Wilske, B., Zeppel, M., Zhang, Y., Zhang, Z., 2011a. A general predictive model for estimating monthly ecosystem evapotranspiration. *Ecohydrology* 4, 245–255.
- Sun, G., Caldwell, P., Noormets, A., McNulty, S.G., Cohen, E., Myers, J.M., Domec, J.C., Treasure, E., Mu, Q., Xiao, J., John, R., Chen, J., 2011b. Upscaling key ecosystem functions across the conterminous United States by a water-centric ecosystem model. *Journal of Geophysical Research* 116, G00J05.
- Sun, G., Sun, O.J., Zhou, G., 2009. Water and carbon dynamics in selected ecosystems in China (Editorial). *Agricultural and Forest Meteorology* 149, 1789–1790.
- Tan, J., Zha, T., Zhang, Z., Sun, G., Dai, W., Fang, X., Xu, F., 2009. Effects of soil temperature and soil water on soil respiration in a poplar plantation in Daxing district of Beijing, China. *Ecology and Environmental Sciences* 6, 2308–2315.

- Thomas, C.K., Law, B.E., Irvine, J., Martin, J.G., Pettijohn, J.C., Davis, K.J., 2009. Seasonal hydrology explains interannual and seasonal variation in carbon and water exchange in a semiarid mature ponderosa pine forest in central Oregon. *Journal of Geophysical Research-Biogeosciences* 114, G04006.
- Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Tank, A.K., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., Soden, B., Zhai, P., 2007. Observations: surface and atmospheric climate change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Vitousek, P.M., 1991. Can planted forests counteract increasing atmospheric carbon dioxide? *Journal of Environmental Quality* 20, 348–354.
- Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society* 106, 85–100.
- Wilson, K.B., Baldocchi, D.D., 2000. Seasonal and interannual variability of energy fluxes over a broadleaved temperate deciduous forest in North America. *Agricultural and Forest Meteorology* 100, 1–18.
- Wilson, K.B., Baldocchi, D.D., Hanson, P.J., 2000. Quantifying stomatal and non-stomatal limitations to carbon assimilation resulting from leaf aging and drought in mature deciduous tree species. *Tree Physiology* 20, 787–797.
- Wright, M.S., Greene-McDowelle, D.M., Zeringue, H.J., Bhatnagar, D., Cleveland, T.E., 2000. Effects of volatile aldehydes from *Aspergillus* – resistant varieties of corn on *Aspergillus parasiticus* growth and aflatoxin biosynthesis. *Toxicon* 38, 1215–1223.
- Xu, J., Chen, J., Brosfokske, K., Li, Q., Weintraub, M., Henderson, R., Wilske, B., John, R., Jensen, R., Li, H., Shao, C., 2011. Influence of timber harvesting alternatives on forest soil respiration and its biophysical regulatory factors over a 5-year period in the Missouri Ozarks. *Ecosystems* 14, 1310–1327.
- Yu, A., Huang, G., Chai, Q., 2012. Effect of different tillage treatments on soil respiration of winter-wheat farmland in oasis irrigated area Northwest China. *Acta Prataculturae Sinica* 21, 273–278.
- Yuste, J.C., Janssens, I.A., Carrara, A., Meiresonne, L., Ceulemans, R., 2003. Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest. *Tree Physiology* 23, 1263–1270.
- Yuan, W., Liu, S., Yu, G., Bonnefond, J.M., Chen, J., Davis, K., Desai, A.R., Goldstein, A.H., Gianelle, D., Rossi, F., Suyker, A.E., Verma, S.B., 2010. Global estimates of evapotranspiration and gross primary production based on MODIS and global meteorology data. *Remote Sensing of Environment* 114, 1416–1431.
- Zhang, J., Song, C., Wang, S., 2008. Shortterm dynamics of carbon and nitrogen after tillage in a freshwater marsh of northeast China. *Soil and Tillage Research* 99, 149–157.
- Zhang, Y., Zhang, Z. Q., Sun, G., Fang, X. R., Zha, T. G., Noormets, A., Chen, J. Q., McNulty, S., Liu, C. F., Chen, L. X., in preparation. Water balance of a poplar plantation forest in Suburban Beijing, China. *Journal of Environmental Management*.